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STUDIES OF PELECYPODA.

BY ROBERT TRACY JACKSON.

THIS paper is a brief summary of some of the more important and interesting facts and conclusions contained in a paper recently published by the author.[1] The leading principles employed in the paper are two: I. Professors Cope's and Hyatt's theory of the acceleration of development, with its corollary that in the young, stages are found, the equivalents of which are to be sought in the adults of ancestral groups. II. That in the mechanical conditions of environment and a study of the life-habits of animals, facts may be gathered which will throw light on the origin and meaning of external and internal anatomical features.[2] In accordance with the above principles, young and adults, living and fossil species of many allied genera were taken up as one common study.

The completed embryonic shell of Pelecypods differs from and is commonly sharply marked off from the succeeding shell growth. This embryonic shell is compared to the protoconch of cephalous molluscs, and as it is bivalved it is termed a prodissoconch. Carrying out the same terminology, the succeeding shell growth is termed a dissoconch. In my paper a prodissoconch is described, or at least mentioned, as existing in thirty-nine genera of Pelecypods.

Prof. Hyatt's classification of stages of growth and decline[3] is considered at length in its application to the Mollusca. Some alterations in that valuable classification were deemed necessary, and are introduced.

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[1] Phylogeny of the Pelecypoda, the Aviculidæ, and Their Allies. Mem. Bost. Soc. Nat. Hist., Vol. IV., No. 8, July, 1890, pp. 277–400, Pls. XXIII.–XXX.

[2] In a paper soon to be published in this journal, I consider some cases of the mechanical origin of structures in Pelecypods.

[3] See this journal for October, 1888.

The development of the oyster is followed from the egg up to the adult. It is a highly modified Pelecypod, and has a very accelerated development. The completed prodissoconch stage of Ostrea (Fig. 1) is an important period in development, and yields facts of much phylogenetic significance. Two adductor muscles exist instead of one, as in earlier and later stages. No foot, but filamentous gills, a velum, and a plain mantle border exist. The anus overlies the posterior adductor muscle, and the velum and mouth lie on the ventral border of the anterior adductor, the normal condition in dimyarian Pelecypods. The larval umbos are directed posteriorly, —a fact of some significance. In all Pelecypods apparently, as in Ostrea, the anterior adductor is developed first, both muscles always being present, as far as known, at the completed prodissoconch stage.

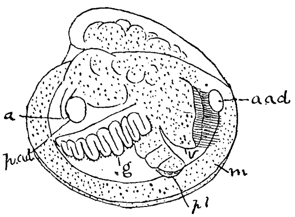

FIG. 1.—*Ostrea virginiana; a ad, p ad*, anterior and posterior adductor muscles; *g*, gills; *v*, velum; *pl*, palps; *a*, anus; *m*, mantle border. X 90 diam.

In the nepionic stages, which succeed the prodissoconch, changes take place rapidly. Fig. 2 is the same specimen as Fig. 1, but three days older. The anterior adductor muscle has disappeared, and the gill filaments are connected ventrally by cross-connecting bars. Later the antero-posterior axis becomes revolved, so that the mouth parts are directed toward the hinge line. An intricate system of cross-connecting bars is built up between the gill filaments, until we find the condition characteristic of the adult. Whereas but a single pair of gills exists in early stages, later two new gills originate, one on the outer side of each previously formed gill. The new gills do not originate simultaneously, but there is a considerable interval, which forms a three-gilled period.

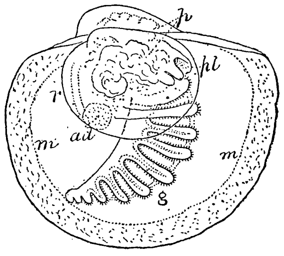

FIG. 2.—*Ostrea virginiana; pl*, palps; *ad*, adductor muscle; *r*, rectum; *g*, gills; *m*, mantle border; *p*, prodissoconch.

There are four distinct periods in the development of the shell of Ostrea: I. The phylembryo[4] stage, with saucer-shaped valves, a straight hinge line, and but slightly developed umbos. II. The completed prodissoconch (Fig. 3), with a curved hinge line, well-developed umbos, nearly equal valves, and without prismatic cellular structure. In *Ostrea edulis* there are teeth similar to those of Nucula on the hinge line of the prodissoconch, but none exist in *O. virginiana.* III. The nepionic period (Fig. 4), with a flat attached and convex free valve. The triangular cartilage pit of Ostrea originates in the initial nepionic stages on the border of the prodissoconch valve (Fig. 5). The right valve of this period has a well-defined prismatic layer. IV. The adult, in which the attached valve is concave and the free valve is flat.

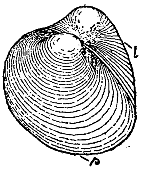

FIG. 3.—Prodissoconch stages of *Ostrea virginiana;* *l*, left, and *r* right valve.

In the Ostreidæ[5] the striking peculiarity of the shell is that the valves are unequal, and also dissimilar. This character is ascribed to the mechanical effects of the condition of cemented fixation acting on a Pelecypod shell. This conclusion is of great value in tracing the genetic relations of attached forms. Differences in the two valves of attached forms may be seen in Spondylus, Hinnites, Mulleria, the Chamidæ, Rudistæ, etc. There is abundant proof that the form is due to the condition of fixation, and not to gravity, as has been maintained. The form induced

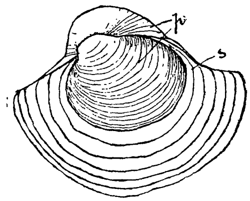

FIG. 4.—*Ostrea virginiana;* *p*, prodissoconch; *s*, spat or nepionic growth.

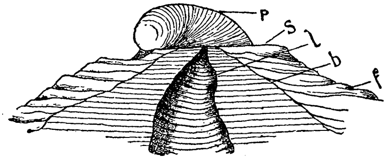

FIG. 5.—*Ostrea virginiana;* tip of left valve; *p*, prodissoconch; *s*, spat or nepionic growth; *l*, cartilage pit; *b*, flange-like extension of shell over object of support.

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[4] A new term, designating an early embryonic stage, yet which is advanced enough to show the characteristics of the class or phylum to which the embryo belongs.

[5] In my paper it is spelled Ostreadæ. In deference to rule, as a family name it should have been spelled as above. See Proc. Am. Ass. Adv. Sc., Aug., 1877.

by cemented fixation is a concave attached valve, a flatter and commonly thinner free valve, an irregularity and assymmetry of growth tending to the displacement of characters normally found in near allies, and, as a general thing, a camerated structure of the shell. The fullest modification in this line of variation is the production of a shell in which the attached valve is cup-shaped, conical, or subcylindrical, as seen in the Chamidæ and Rudistæ. In this group as a whole, and in the progressive stages of growth of its extremest members, all transitions may be followed between a simple ostreiform or exogyriform shell and the most highly modified conical type. The Ostrea form is the first step in this line of variation, the Exogyra form is the second step, and the Hippurite form is the last step. The equal impact of moving water on all sides of the attached organism is believed to be the chief factor in inducing this form, but aided by correlated forces as briefly discussed in my paper.

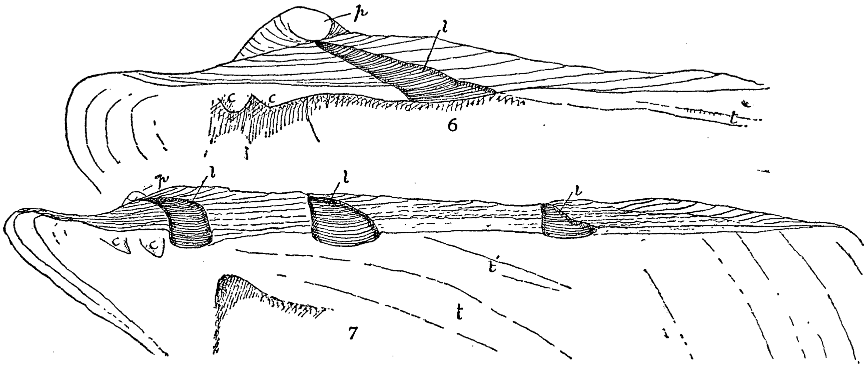

FIG. 6.—Young *Perna ephippium*, right valve ; *p*, prodissoconch ; *l*, cartilage pit ; *c*, cardinal, and *t*, lateral, teeth. X 90 diam.

FIG. 7.—*Perna ephippium*, older than Fig. 6, with several cartilage pits ; lettering as above. X 24 diam.

It is considered that Ostrea probably descended from Perna, or a close common ancestor of the two genera. The bases of likeness are the anatomy of the soft parts, shell structure, the prodissoconch, and other features in the development of both genera. The differences are mainly ascribed to the effects of the condition of fixation in Ostrea.

Perna has a prodissoconch closely like that of Ostrea. The byssal sinus originates in the initial stages of dissoconch growth. In young Perna (Fig. 6) a single triangular cartilage pit exists as in Ostrea. In later growth new pits originate on the ligamental line (Fig. 7). They, too, are triangular at first, but when the sides of the triangles have attained a certain degree of divergence they are produced perpendicularly, which is the condition found in the adult. The nepionic stage of Perna (Fig. 8) is subrhombic in form, and the anterior auricle descends directly from the limits of the prodissoconch. The form of this stage is comparable to that found in early Paleozoic Aviculoids. It is compared to *Rhombopteria glabra* sp. Barr., from the Silurian.

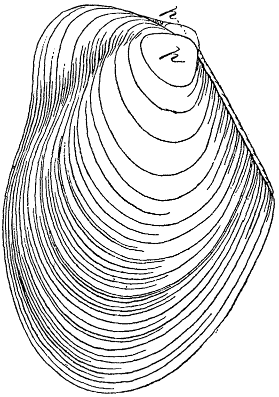

FIG. 8.—Young *Perna ephippium; p*, prodissoconch. X about 37 diam.

In Avicula we find a prodissoconch like that of Perna and Ostrea, and, as in those genera, it is traceable in origin to the nuculoid radical which forms the basis of our genealogical table. The nepionic stage of Avicula (Fig. 9) is subrhombic in form, and is referable in origin to early Aviculoids. It is compared to *Rhombopteria mira* (Fig. 16), from the Silurian. A later stage of Avicula (Fig. 10) differs from the nepionic and adult periods, and is comparable to the Devonian genus Leptodesma, which is the third step up in the phylogeny of the Avicula series.

A prodissoconch and nepionic stage similar to those of Avicula are described in many allied genera, which are Meleagrina, Monotis, Pseudomonotis, Oxytoma, Cassianella, and Vulsella.

Pecten irradians presents an interesting subject for study. Its life-habits are varied and striking. Its stages in growth, both in the soft parts and the hard, present a remarkable series of high phylogenetic significance. At the completed prodissoconch stage Pecten is doubtless dimyarian, and crawls on the ventral border of the valves by means of an active foot. It may also have a velum at that stage, and be capable of swimming by means of that organ. In the nepionic stage the foot is of relatively great size, mobile and prehensile. It extends through a special notch in the right valve (Fig. 12), this being the side on which the foot exerts pressure in the act of crawling. This notch is a necessary mechanical consequence of the conditions of the case. At a later stage in Pecten we find that the early free crawling condition is abandoned, and the animal adopts the habit of byssal fixation, which is more or less adhered to until the animal is two to three centimetres in height; but was not observed in adult *Pecten irradians*.[6] Although the swimming habit of *Pecten irradians* is more or less exercised from the nepionic stages up, it is essentially the life-habit of the adult, for then the crawling and byssal habits are abandoned and the foot is atrophied. The swimming of Pecten is most active, and in the anatomy we find a most perfect adaptation of parts to the requirements of this peculiar habit.

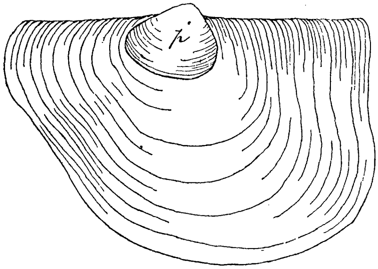

FIG. 9.—Young *Avicula sterna*, umbonal area of valve, showing (*p*) prodissoconch and succeeding nepionic growth.

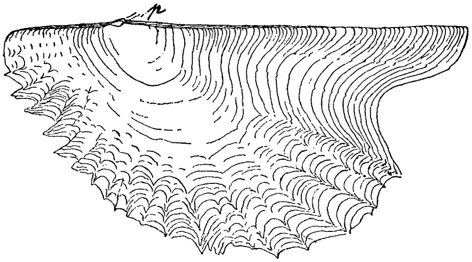

FIG. 10.—Young *Avicula sterna*, showing later stage of growth.

In the shell of Pecten (Figs. 11, 12) the prodissoconch is sharply defined, as in the genera already mentioned. It is directly referable in shell structure and in the inferred soft parts to to the nuculoid radical of the group. The nepionic stage (Figs. 11, 12), is subrhombic in form, has no ears, and is a very striking period of growth. The right valve has a byssal sinus which originates with the nepionic stage as in Perna and Avicula, and a tooth exists on the margin of the notch. This stage is closely like the same stage of Perna (Fig 8) and Avicula (Fig. 9), and is traceable in origin to the same ancestral type, Rhombopteria (Fig. 16). The right valve of this stage of Pecten possesses a well-defined layer of prismatic tissue, though it is early lost.

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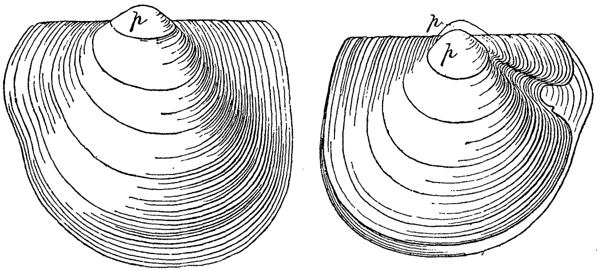
[6] I recently dredged near Eastport, Me., adult specimens of *Chlamys islandica* which were attached by a byssus.



FIGS. 11, 12.—Young *Pecten irradians*, viewed from the left and right sides; *p*, prodissoconch. X about 37 diam.

This is a good example of accelerated development, for prismatic tissue is characteristic of the adults of the Aviculidæ, from which group the Pectinidæ were derived.

In a later stage of growth of Pecten (Fig. 13) we find important changes in form, which mark the beginning of features characteristic of the family. The hinge line is longer and terminated by slightly developed ears, plications originate in both valves, and the byssal notch is strongly marked. This stage is referable

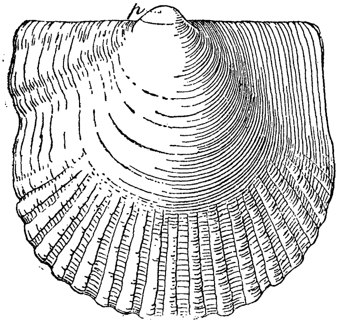


FIG. 13.—Young *Pecten irradians; p*, prodissoconch. X 30 diam.

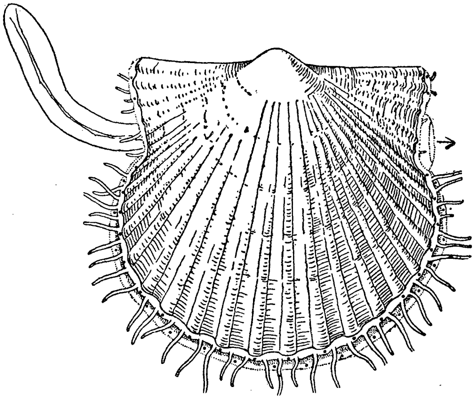


FIG. 14.—*Pecten irradians*, still older; showing foot, tentacles, eyes, and excurrent pseudosiphon. X 12 diam.

in origin to Pterinopecten, a Devonian genus which is adopted as the base of the family of the Pectinidæ. At a still later stage (Fig. 14), the hinge line is relatively shorter than in Fig. 13, yet longer than in the adult. The ears are well pronounced. This stage is comparable to Aviculopecten (as amended by Prof. James Hall), which is the second step in the Pecten series.

Similar stages to those described in *Pecten irradians* have been observed in several other species. In the young of *Pecten magellanicus* there is ornamentation of the shell strikingly like that seen frequently in Aviculopecten.

Hinnites is pecteniform in its nealogic stage, and shows graphically the change in form induced when it becomes attached and assumes the ostrean features characteristic of the adult. Spondylus has a prodissoconch like Pecten, and in its nepionic stage is pecteniform as observed in five species, proving its origin in that group. It early becomes attached and assumes the ostrean form. Plicatula becomes attached at the close of the prodissoconch stage, and at once assumes the ostrean form; thus as in Ostrea nepionic characters are eradicated which might, if existent, show distinct phylogenetic stages. It is the furthest removed from Pecten of its series, because it earliest and most completely assumes the ostrean form.

In Anomia the form of shell and peculiarities in the soft parts may fairly be ascribed to adaptation to the environment, rather than to genetic connections of the group. In the early nepionic stage Anomia is freely locomotive, with a highly active foot. At this age byssal attachment is voluntary, and is frequently abandoned. The relations of the muscles, which are ambiguous in the adult, are clear in the young. The calcareous plug is composed of consolidated parallel ridges of lime. In the young these ridges are seen to be made up by the amalgamation of calcareous discoid points. The several points are directly comparable to the discoid points of fixation of the byssal threads in Pecten, Mytilus, etc. The prodissoconch of Anomia is described in two species. It differs from the prodissoconch of the previously mentioned genera in possessing a slight byssal sinus in one or both valves, according to the species, thus showing a very accelerated development. During the nepionic stage the byssus becomes enclosed by progressive deepening of the byssal sinus and circular growth of the right valve. In later growth extensive resorption of the shell progressively enlarges the byssal foramen. The right valve of *Anomia glabra* is thinner than the left valve, and differs also in being almost entirely composed of prismatic tissue.

In the section "Studies of a Few Other Genera" the young of Pelecypods more or less remotely separated from the Aviculidæ are considered. In these genera the umbos of the prodissoconch are directed anteriorly relatively to the larval anatomy, excepting in Nucula, Tellina, and the Unionidæ, in which last group umbos are not developed. In all genera excepting the Unionidæ the nepionic stage does not have a prismatic layer. In genera of the Aviculidæ and allies, on the contrary, we find the umbos of the prodissoconch are directed posteriorly relatively to the larval anatomy (Fig. 1), and the nepionic stage has a layer of prismatic tissue, although this may disappear in later growth.

In genera of the Mytilidæ and Arcidæ we find a well-defined prodissoconch and nepionic stages, which are traceable to ancient fossil representatives of the families. In three genera of the Unionidæ studied the completed prodissoconch is of the same size and form as the glochidial stage. In structure it has not progressed beyond a modified condition of the phylembryonic stage. It is a specialized type, owing its peculiarities apparently to parasitism and correlated larval adaptation. A prodissoconch and nepionic stages are described in Echinochama, Sphærium, Petricola, Venus, Tottenia, Scrobicularia, and Saxicava. The prodissoconch is mentioned without description in a few other genera. In *Mya arenaria* a considerable description is given of the byssal habit, development of the siphon, and the shell. These present features of phylogenetic interest.

In the development of the shell of Pelecypods the phylembryonic stage has a straight hinge line, which apparently represents a primitive condition common to the whole class. This form appears to be the natural mechanical outcome of its derivation from a primitive univalvular ancestral type. The next step in the development of the Pelecypod shell is the curving of the hinge line, the centralization of connecting tissue and teeth in the middle of the hinge line, and the development of umbos.

The characters described in the prodissoconch of the Aviculidæ and their allies are found combined in a remarkable degree in the ancient genus Nucula, which, though living to-day, extends back to early Paleozoic formations. It is probable that Nucula, or a nuculoid form, is the type we are seeking as the ancestral radical represented by the completed prodissoconch in the development of Avicula, Perna, Ostrea, Pecten, and their allies. The fact that Nucula is found in the Lower Silurian, and still lives without sufficient changes in form to make these extremely separable forms in time generically separable, argues for a high antiquity for this genus. It was so firmly established in its earliest-known forms, it must at that time have been an ancient genus.

The nepionic stages of Avicula, Perna, and Pecten (Figs. 8, 9, and 11) agree closely in form, and are referable to an early, simple aviculoid type, Rhombopteria (Fig. 16). Therefore, that genus is adopted as the basis of the Aviculidæ, being the first step up from the nuculoid radical of the group. From Rhombopteria, Leptodesma leads up to Avicula, forming the central stock of the family. From the Avicula stock many side issues arise, as Meleagrina, Pseudomonotis, Cassianella, Malleus, and others. These are like Avicula (Fig. 9) in the nepionic stage, but in later growth depart from the typical form of the stock. Perna is an important issue from Avicula, which it resembles in the nepionic stage. Gervillia and the Inoceramus group are modified forms from the Perna stock. The Ostreidæ are considered a modified branch from the Perna stock, which owes its peculiar features chiefly to the effects of fixation. Ostrea is the base of its group, and Exogyra the extreme, because it is the most highly modified by the adopted habit of attachment.

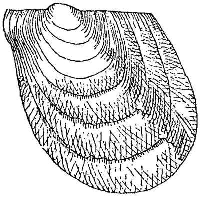


FIG. 16.—*Rhombopteria*[7] *mira* sp. Barr. Upper Silurian (after Barrande).

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[7] A new genus, proposed in my paper for an ancient simple group of aviculoid shells.

From Leptodesma-like forms the Pinnidæ are probably derived. This is considered a degradational group on account of the high development of the anterior adductor (a larval character), prismatic structure, and other peculiarities of some members. The Pterinea group is considered a side issue from the Rhombopteria stock. Pterinopecten is an important branch from the Rhombopteria stock. In the young it closely resembles Rhombopteria. It forms the base of the Pecten series. Aviculopecten is the next ascendant step in the Pecten series. In stages of growth it resembles, first, Rhombopteria; second, Pterinopecten. Pecten, the representative of the family, is the summit of the stock. As we have shown, the prodissoconch resembles the nuculoid radical. The first nepionic stage resembles Rhombopteria; the second and third nepionic stages, resemble respectively Pterinopecten and Aviculopecten. Lyriopecten and Crenipecten are considered side issues from Aviculopecten. From the Pecten stock important issues are given off. These are the Hinnites, Lima, Amusium, Anomia, and Dimya groups.

The phylogenetic relations of the Aviculidæ and allies are considered in more or less detail in the last section of my paper, which is closed by a tabular view representing graphically the various genetic relations expressed.